

Karyotype of the Agamid Lizard *Lyriocephalus scutatus* (L., 1758), with a Brief Review of the Chromosomes of the Lizard Family Agamidae

by

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The lizard family Agamidae has not been well-studied karyotypically and until recently (Gorman, 1973) the few taxa sampled did not indicate great chromosomal diversity. We report here the karyotype of *Lyriocephalus scutatus*, the first member of the diverse agamid radiation of the Asian equatorial region to have been karyotyped. The karyotype of this species, a diploid number of 30 chromosomes, is also the first example of a karyotype in the family Agamidae which has a number of chromosomes deviating significantly lower than the primitive lizard karyotype of 36 chromosomes.

At the time of the most recent review of agamid chromosomes (Gorman, 1973), only nineteen species representing seven genera had been karyotyped. With so few data, chromosomes could not contribute to phylogenetic hypotheses of the Agamidae. However, several recent karyological studies of agamids (Gorman and Shochat, 1972; Sokolovskii, 1974, 1975) allow us to suggest two different chromosome patterns which may be of taxonomic importance at the generic level.

Materials and Methods

One sexually mature male *Lyriocephalus scutatus* was karyotyped after pre-treatment with colchicine. Cells were spread by air drying smears of methanol: acetic acid (3 : 1) fixed suspensions of testis, spleen and bone marrow tissues. Only metaphase chromosomes from the bone marrow suspension were suitable for examination. Nine cells were examined and photographed at a microscopic magnification of 1000X, and measurements were taken directly from photographs additionally enlarged 230X. The chromosome pairs were ranked by size and average percentage lengths for each pair were calculated relative to the longest pair. Arm length ratios indicating centromere position were obtained by dividing the long arm by the short arm.

Results

Lyriocephalus scutatus has a diploid number of 30 chromosomes ($2n = 30$) and a fundamental number of 46, of which 12 chromosomes (pairs 1

through 6) are rather large and 18 (pairs 7 through 15) are relatively small (Fig. 1). No heteromorphic pairs of chromosomes indicating a sex chromosome were evident in this single male.

Considering the macrochromosomes in order of size, pair one is metacentric with an arm ratio of 1.12. Pair two is conspicuously submetacentric with an arm ratio of 1.89, the long arm nearly twice the length of the short arm, and is only 10.5 % shorter than pair one. Pairs three and four are metacentric, similarly sized and are not easily distinguished, and have arm ratios of 1.15 and 1.11 and percentage lengths of 70.7 % and 65.4 % respectively. Pair five is metacentric and distinguishably shorter than pair four, having a percentage length of 56.2 % and an arm ratio of 1.12. Pair six is metacentric and conspicuously shorter than pair five, having a percentage length of 35.1 % and an arm ratio of 1.13.

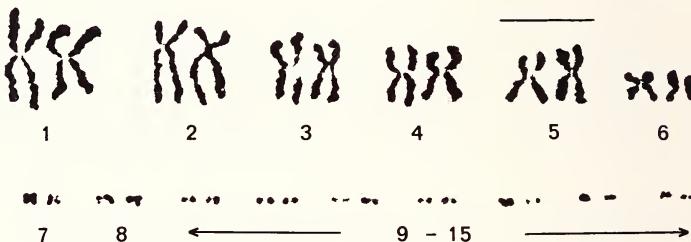


Fig. 1: Karyotype of *Lyriocephalus scutatus* ($2n = 30$), ZFMK 18813, male.
Length of line is 0.1 mm.

The first two pairs of microchromosomes are definitely metacentric with arm ratios of 1.07 and 1.11 respectively. In several cells pair seven appeared to be submetacentric, the long arm twice the length of the short arm, but this was not consistently observed. Pair seven is conspicuously large with a percentage length of 20.5 %. Pair eight is easily distinguished from the remainder of the microchromosomes and has a percentage length of 12.2 %.

Microchromosome pairs nine through fifteen appear to be acrocentric and uniformly sized, the percentage lengths ranging from 7.5 % to 10.1 %. However our preparations do not resolve their structures well enough to allow them to be unequivocally paired.

Discussion

A chromosomal arrangement with a $2n$ of 36, with 12 metacentric macrochromosomes and 24 microchromosomes was hypothesized by Gorman (1973) to be the primitive lizard karyotype. The high frequency of occurrence of this chromosomal arrangement and of karyotypes easily derived

from this arrangement within most lizard families positively argues for this hypothesis. Williams and Hall (1976) have strengthened this hypothesis with additional chromosomal data for the Iguanidae, the karyotypically best studied lizard family.

Very few agamid species had been karyotyped at the time of Gorman's review in 1973, and a chromosomal arrangement characterizing the family could not be concluded. Nine species representing four genera, *Uromastyx*, *Leiolepis*, *Calotes* and the *Stellio* section of *Agama* have a $2n = 36$ karyotype. There are questionable and conflicting literature reports for the exact number of microchromosomes for some of these species, undoubtedly attributable to poor preparations. Also, one species *Leiolepis triploidea* has a triploid chromosome complement, $3n = 54$, and is apparently parthenogenetic (Hall, 1970; Peters, 1971).

The remainder of these karyotyped agamids, nine species representing four genera, *Sitana*, *Phrynocephalus*, *Japalura* and the *Trapezus* and *Agama* sections of *Agama*, have a much higher number of chromosomes, $2n = 44$ —48. This chromosomal arrangement is easily derived from the primitive $2n = 36$ karyotype by Robertsonian fission of the macrochromosomes and subsequent minor modifications including fusion or loss of microchromosomes and inversions of the acrocentric macrochromosomes, creating small submetacentric chromosomes.

Several additional species of *Agama* and *Phrynocephalus* have recently been karyotypically examined. Sokolovskii (1974) reported the chromosome complements of eight species of the large and diverse genus *Phrynocephalus*, representing most of the species groups. These species have $2n = 46$ or 48 karyotypes, and are distinguishable from each other by variation in centromere position and development of submetacentric macrochromosomes. Sokolovskii (1975) also studied the chromosomes of five asiatic species of the genus *Agama*, four representing the *Stellio* section and one the *Trapezus* section. The karyological data for these species, together with previous data for species of *Agama* karyotyped by Gorman and Shodhat (1972), demonstrates the existence of two different types of karyotypes within the genus *Agama*, as currently taxonomically defined. Seven species, *atricollis*, *caucasica*, *erythrogaster*, *himalayana*, *lehmanni*, *stellio* and *tuberculata*, all possess the primitive $2n = 36$ karyotype. These species also constitute one-third of the species of the *Stellio* section of *Agama*, the whorl-tailed agamas distributed primarily in south-western and central Asia. On the basis of numerous morphological characters (Moody, unpublished), this species group appears to be monophyletic and cladistically worthy of generic rank. The karyological data support this view. The remainder of the *Agama* species have a much different karyotype, $2n = 44$ —48, resembling that of *Phrynocephalus*. These species represent

three distinct species groups within the genus *Agama*, but the karyotypes do not delimit these groups.

One group of agamid species representing four genera having relatively little in common phenetically possess a diploid karyotype of 12 metacentric macrochromosomes and 24 microchromosomes. The distribution of this karyotype among the agamids suggests widespread occurrence and primitiveness, which is consistent with the hypothesis that this karyotype is ancestral for all lizards (Gorman, 1973, Williams and Hall, 1976). Two of the above genera, *Leiolepis* and *Uromastyx*, also possess several morphological characters suggesting relative primitiveness within the family Agamidae (Moody, unpublished), corroborating the primitive karyotype hypothesis.

A second group of agamids, 18 species representing four genera, have in common a karyotype of 24 acrocentric macrochromosomes and 24 microchromosomes, or a minor modification of this pattern, which has probably been derived from the primitive $2n = 36$ karyotype by Robertsonian fission. Whether this derived karyotype has been the result of a single evolutionary event, requiring that these four genera share a common ancestor, cannot be hypothesized using only karyological data.

Lyriocephalus scutatus represents a third pattern of chromosomal variation within the Agamidae, retainment of the 12 macrochromosomes but significant reduction in the number of microchromosomes. All microchromosomes, including the largest, of the agamid species with a $2n = 36$ karyotype, usually are acrocentric. In *Lyriocephalus*, the two largest pairs of microchromosomes are not only substantially larger than the other microchromosomes, but they are also metacentric. Possibly they are the products of Robertsonian fusion of four pairs of smaller acrocentric chromosomes. However, this hypothesis can only be confirmed by discovering detailed chromosome markers, for example, banding sequences rendered visible by improved staining techniques, and by cytogenetically studying other closely related species in order to homologize the microchromosomes.

Lyriocephalus also has a distinctly large submetacentric chromosome which may be a useful character in taxonomically comparing species presumably related to *Lyriocephalus*. Deraniyagala (1953: 59) proposed the new subfamily Lyriocephalinae, which includes *Lyriocephalus*, *Cophotis* and *Ceratophora*, three genera endemic to Ceylon. However, the morphological characters he selected for defining this taxon are not unique to these agamid genera, and do not include characters considered conservative by most workers and useful for predicting phylogenetic relationship. The distinct karyotype of *Lyriocephalus* may prove useful in testing the hypothesized relationship with *Cophotis* and *Ceratophora*, and for suggesting a cladistic sister group among the remaining Asian agamid genera.

Acknowledgements

We are grateful to Bernd Schulz, Moers, for providing the specimen of *Lyriocephalus scutatus* for karyotyping, and to Wolfgang Böhme, Museum Alexander Koenig, Bonn, for constructively commenting on this manuscript. The senior author especially thanks the Deutscher Akademischer Austauschdienst for financially supporting his studies in Germany with a stipend.

Summary

1. *Lyriocephalus scutatus* has a $2n = 30$ karyotype, with two submetacentric and ten metacentric macrochromosomes and four metacentric and fourteen acrocentric microchromosomes. This chromosomal arrangement, compared with other karyologically studied agamids, is uniquely different.

2. A survey of the recent karyological literature for the Agamidae demonstrates that a $2n = 36$ karyotype with 12 metacentric macrochromosomes and 24 microchromosomes is the most frequently observed. This observation support the hypothesis of Gorman (1973) and Williams and Hall (1976) that the $2n = 36$ karyotype is primitive for lizards.

3. A chromosomal arrangement of $2n = 48$ which has been apparently derived from the $2n = 36$ karyotype by Robertsonian fission of the 12 macrochromosomes, is the second most frequently observed among the agamids. This karyotype is characteristic of the genus *Phrynocephalus* and of several species groups in the genus *Agama*.

4. Both chromosomal arrangements, $2n = 48$, are found in the large and diverse genus *Agama*, the primitive karyotype characterizing the *Stellio* section. This major chromosomal difference, together with correlated morphological attributes, supports the view that the *Stellio* group of species be recognized as a separate taxon.

Zusammenfassung

1. Unter den bisher cytogenetisch untersuchten Agamen weist *Lyriocephalus scutatus* einen einzig dastehenden Karyotyp auf: $2N = 30$, NF := 46, mit 2 submetazentrischen und 10 metazentrischen Makrochromosomen und 4 metazentrischen und 14 akrozentrischen Mikrochromosomen.

2. Die neuere Literatur über die Chromosomen der Agamidae zeigt, daß der $2N = 36$ Karyotyp mit 12 metazentrischen Makrochromosomen und 24 Mikrochromosomen am häufigsten vertreten ist. Das spricht für die Hypothese von Gorman (1973) und Williams und Hall (1976), daß $2N = 36$ der primitive Eidechsen-Karyotyp ist.

3. Die Chromosomenzahl $2N = 48$, vermutlich vom $2N = 36$ Karyotyp durch Aufspaltung der 12 Makrochromosomen abgeleitet, ist das zweite häufig vertretene Muster bei den Agamen, charakteristisch für die Gattung *Phrynocephalus* und zahlreiche Artengruppen der Gattung *Agama*.

4. Beide Chromosomenzahlen, $2N = 36$ und $2N = 48$, sind innerhalb der großen, diversen Gattung *Agama* vertreten, wobei der primitive Karyotyp die

Artengruppe *Stellio* charakterisiert. Die klar unterschiedenen Chromosomenzahlen sprechen ebenso wie morphologische Merkmalsdifferenzen für die Ansicht, daß die Artengruppe *Stellio* ein eigenes Taxon darstellt.

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Zeitschrift/Journal: [Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.](#)

Jahr/Year: 1978

Band/Volume: [29](#)

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Artikel/Article: [Karyotype of the Agamid Lizard *Lyriocephalus scutatus* \(L.. 1758\), with a Brief Review of the Chromosomes of the Lizard Family Agamidae 165-170](#)